Shifts in Patterns of Microhabitat Occupation by Six Closely Related Species of Mosses Along a Complex Altitudinal Gradient

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Summary. Changes in patterns of microhabitat occupation were examined for six closely related moss species (family Polytrichaceae) found growing together along a complex altitudinal gradient on the northeast face of Mount Washington, New Hampshire. Little evidence could be found to support the hypothesis that the relative distributions of these six moss species were determined by competitive interactions occurring among them. Instead, the data support the hypothesis that changing patterns in the relative distributions of these six moss species result from differences in microhabitat availability among sites. The moss species appear to behave in an opportunistic manner, occupying a wide array of microhabitats as these microhabitats become available to them.

Introduction

Previous considerations of niche relationships among both plant and animal species have emphasized the importance of the role of competitive interactions among co-occurring species in determining patterns of resource utilization or habitat occupation (e.g., Pianka 1975, 1976; Schoener 1974; Platt and Weis 1977; Werner and Platt 1976; Pickett and Bazzaz 1976; Parrish and Bazzaz 1976, 1978). This emphasis is a natural and anticipated response to the original formulation of the n-dimensional niche concept by Hutchinson (1957, 1978), in which a distinction was made between the 'fundamental' niche of a species, defined under conditions of isolation and determined by the genetically programmed physiological tolerances of the organism; and the 'realized' niche of the species, representing a contraction in niche space – presumably caused by unsuccessful competition with other species in portions of the species' fundamental niche. The emphasis on competition as a regulating mechanism was strengthened in the work of Vandermeer (1972) in which he introduced new definitions of the two niche categories; referring to the 'fundamental' niche of a species as its pre-interactive niche, and the realized niche of a species as its post-interactive niche.

A certain ambiguity persisted in the definition of the niche which related to the scale on which observations of species behavior or distribution were examined. This ambiguity has been discussed by Whittaker et al. (1973), who suggest that a distinction be made between the distribution boundaries of a species which are defined within a homogeneous habitat (i.e., niche boundaries

as first presented by Hutchinson (1957)), and the distribution boundaries of a species which are defined across complex environmental gradients, which they termed 'ecotope' boundaries.

As the biotope expands to include an increasing array of habitats, the ecotope spaces defined within can be viewed as converging on a definition of the species fundamental niche. Within any one homogeneous portion of the biotope space, the species niche may be locally defined, and this definition may be expected to vary among samples observed in different portions of the biotope space.

While a rather large number of studies are available which have investigated either niche (i.e., ecotope) relationships among species across complex environmental gradients (e.g., Whittaker 1967; Bratton 1976; Pianka 1973), or niche relationships within single habitats (e.g., MacArthur 1958; Platt and Weis 1977), few studies have sought to explore changes in niche relationships among members of a species array within different visually homogeneous habitats, located at intervals along a complex environmental gradient (e.g., Diamond and Marshall 1977). One such study by Cody (1978) on the distribution ecology of *Haplopappus* and *Chrysothamnus* species indicates significant shifts in niche position at different points along north-facing granitic slopes. The following questions may be asked. Do shifts in niche position of species along complex environmental gradients always result from changing competitive interactions among species; or may these shifts, in certain cases, be simply explained by the differential availability of particular resource or habitat categories at different points along the environmental gradient?

The purpose of this study was to determine those factors significant in the development of patterns of distribution and association among members of a closely related species group examined along a complex altitudinal gradient which spanned a wide diversity of habitats. The study was conducted along an 1,600 meter altitudinal gradient on the northeast face of Mount Washington, New Hamphire (71° 18′W, 44° 16′N). During preliminary visits to the area it was observed that certain species within the bryophyte community exhibited broad patterns of distribution along the altitudinal gradient. Of particular interest were six closely related moss species belonging to the family Polytrichaceae (star mosses) which were observed growing together, in a variety of combinations, throughout the length of the transect. The data presented below examine the patterns of distribution of the species along a number of different habitat parameter axes within nine different sites distributed along the altitudinal gradient (niche analysis). The patterns of distribution of the six species along these habitat parameter axes on the mountain, considered as a whole (i.e., ecotope analysis sensu Whittaker et al. 1973), have been considered in detail elsewhere (Watson, in press).

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The Study Organisms

The following species were the focus of this study: *Polytrichum commune* Hedw., *P. juniperinum* Hedw., *P. piliferum* Hedw., and *Polytrichastrum formosum* (Hedw.) G.L. Smith, *Pa. pallidisetum* (Funck) G.L. Smith, and *Pa. alpinum* (Hedw.) G.L. Smith. The separation of the group into two genera is the result of a recent revision of the family (Smith 1971). Assignment of a species to a particular genus is based, in part, upon morphological characteristics of the ephemeral sporophyte. These generic characters possess no intuitive ecological significance.

The leafy gametophytes (=dominant life phase) of these six species are morphologically similar. Assignment of individual vegetative stems to a particular species is based, in part, upon the structure of the terminal cells of the leaf lamellae. The terminal cells of the lamellae are believed to act to control water loss from the inter-lamellar spaces during periods of mild water stress, and are, in this sense, similar in function to the stomates of higher plants (Sarafis 1971). This latter array of taxonomic characters, used in specific assignment, has potential significance in determining the competitive success of individual species in different microhabitats (see Watson 1974).

Methods

The study was conducted on the northeast face of Mount Washington, New Hampshire (71° 18'W, 44° 16'N), along an 1,600 meter altitudinal gradient which spanned a wide diversity of habitats. Nine sites were established along the gradient, spaced so as to include each of the major vegetation types represented on the mountain. A vegetational description of the sites, based upon the species composition of the overstory canopy is provided in Table 1.

Within each site a visually homogenous area measuring approximately 100 × 200 m was sampled at random. At each sampling point a quadrat measuring 50 × 50 cm and divided into a grid of 25, 10 × 10 cm subsample units was placed on the ground. A total of 25 sample quadrats containing one or more of the subject species was located at random at each study site. In 1972, the number of 'empty' quadrats encountered (i.e., those which did not contain any of the subject species) was not recorded; thus data from that year is expressed solely in terms of the 25 quadrats which were actually sampled. In 1973, the number of 'empty' quadrats was recorded and these data used to determine the actual % cover of the different vegetation types in the herbaceous layer at each site.

Estimates of % cover were determined for the herbaceous layer at each site for all vegetational classes exhibiting canopy development within 35 cm of the ground. Percent cover was determined for each sample quadrat by counting the fraction of subsamples within a sample quadrat occupied by each of six vegetational classes: 1. polytrichaceous mosses, 2. other bryophytes, 3. herbs, 4. woody plants, 5. bare ground (available space) – including soil, gravel and rock, 6. undecayed leaf litter (held space).

Within each sample quadrat, a single 100 sq cm subsample was selected at random. Each subsample was removed in its entirety for analysis by cutting the turf block from the substrate. Individual samples were placed in paper bags and returned within a week to the laboratory where they were air-dried and stored at 15° C. A total of 189, 10 × 10 cm subsamples were analyzed; 15 each collected at sites 1 and 8, 14 at site 2, 22 at site 3, 23 at site 4, and 25 subsamples each at sites 5–7 and site 9. Twenty-

Table 1. Description of sites

The position of the sites, with the exception of site 9, approximate the locations established by Forman (1969)

site 1: alpine – 1,864 m (6,110 ft) – alpine meadow, dominants are: *Carex bigelowii, Juncus trifidis, Polytrichum juniperinum.* Areas of herbaceous cover clearly separated from moss turfs, meadow littered with cobble, slope level

site 2: alpine – 1,676 m (5,500 ft) – alpine meadow with scattered krummholz vegetation, dominants include: *Juncus trifidis, Vaccinium uliginosum, Polytrichum juniperinum,* slight slope

site 3: krummholz – 1,293 m (4,240 ft) – krummholz on exposed shoulder, xeric, dominants include: *Vaccinium* spp. *Diapensia lapponica, Abies balsamea, Picea rubens.* Area is quite barren, consisting of a gravel substrate interspersed with cobble; vegetation patchily distributed, slope level

site 4: coniferous – 1,173 m (3,845 ft) – low coniferous forest, trees less than 20 ft tall, with coniferous understory, dominants are: *Abies balsamea, Picea rubens, Betula papyrifera.* The canopy contains scattered openings, slope gradual (< 50)

site 5: coniferous – 938 m (3,075 ft) – coniferous forest, dominants are: *Abies balsamea, Picea rubens. Oxalis montana* constitutes the dominant herbaceous cover. The substrate is loosely compacted humus and rotting tree trunks, locally unstable, slope approximately 15°

site 6: coniferous-deciduous – 854 m (2,800 ft) – mixed forest with scattered spruce understory, dominants include: *Betula lutea, Betula papyrifera, Picea rubens, Abies balsamea. Oxalis montana* is the primary herbaceous ground cover, although there is an increase in the diversity of the herbs. Substrate compact, mixed deciduous-coniferous litter, slope approximately 15°

site 7: deciduous-coniferous – 798 m (2,615 ft) – deciduous forest, with increased development of the understory, dominants include: *Betula lutea, Fagus grandifolia, Acer saccharum* and scattered individuals of spruce and fir. Dominant ground cover *Lycopodium lucidulum.* Boulders scattered across slope, slope approximately 20°

site 8: northern hardwood – 552 m (1,810 ft) – deciduous forest with well developed deciduous understory, dominants include: *Fagus grandifolia, Betula lutea,* and in the understory *Acer saccharum, Acer spicatum, Viburnum alnifolium.* Substrate heterogeneous, composed of organic litter and areas of mineral sediment washed down during spring floods, slope slight

site 9: successional field – 290 m (950 ft) – an open field dominated by grasses and herbs. Patches of *Fragaria virginiana* locally abundant. Surface undulates, with accumulation of gravel in the depressions where there are concentrations of *Cladonia* spp., non-sloping

Site 9 was not on Mount Washington but was several miles north in the flood plain of the Peabody River. It was established in order to provide a comparison with the "open" sites above treeline (see Watson in press)

nine percent (54) of the 189 subsamples contained stems of two or more of the sample species growing intermixed.

Patterns of microhabitat occupation for each of the six species, at each of the nine sites, was examined along the altitudinal gradient with respect to four habitat parameter axes (i.e., substrate, soil texture, soil pH, and % incident light). These habitat parameters were viewed as potentially limiting to the relative distributions of the six species both within and between sites. The following data were collected from each of the subsample quadrats.

Substrate. The substrate from which an individual subsample was removed was assigned to one of the following 5 categories at the time of collection: 1. bare ground – including gravel; 2. turf – composed of decaying moss; 3. litter – consisting of other decayed plant material; 4. wood – including living roots as well as decaying stumps and logs; 5. rock – including those rocks covered by a thin layer of soil or litter.

Soil Texture. In each subsample, the soil directly associated with the moss rhizomes was separated and a portion sent for analysis to the Soil Laboratory of the Connecticut State Agricultural Experiment Station, New Haven, CT. Each sample was assigned, by them, to one of the following 8 soil texture classes arranged in an order which proceeds from poorly drained organic to well-drained highly mineralized soils: 1–organic, 2–very fine sandy loam, 3–fine sandy loam, 4–sandy loam, 5–coarse sandy loam, 6–loamy sand, 7–loamy coarse sand, 8–coarse sand.

Soil pH. A portion of the soil which was obtained as described above was passed through a 2 mm sieve and air-dried a minimum of 24 h. To determine soil pH, 1 gm of sieved soil was suspended in a sufficient volume of double distilled water to form a slurry. The slurry was placed on a shaker for 15 min after which the soil was allowed to settle. PH was read on a Beckman Zeromatic pH meter (sensitivity 0.01 pH unit). Values were rounded to the nearest 0.1 pH unit.

Percent Incident Light. Each subsample was assigned a light index value between 1 and 10, based upon the overstory canopy structure above the sample quadrat from which the subsample was removed. This index was then converted to a measure of % incident light by the following procedure.

Relevant light index categories were identified within each site. A mean value for % incident light for each of the index categories was determined by averaging from 3–10 measures of % incident light/index category/site. Percent incident light was measured using a Lamda Measuring Instrument L1-185 Radiometer equipped with a sensor-pyranometer L1-200S (Lambda Corp., Lincoln, Nebr.). The full visual spectrum was monitored and read in watts m^{-2}. All measures were taken in a single day in June, when canopy development was almost complete, and the mosses were actively growing (see Watson 1975).

Percent incident light was computed as (light at surface of the moss canopy/light at the surface of the overstory canopy) $\times 100$. Sites 4–8 possessed well-developed tree canopies. At these sites a series of 5 light meter readings were taken outside the overstory, both before and after readings were taken within the overstory canopy. These 10 readings were averaged and the mean used in the denominator of the equation given above. The numerator was obtained from measurements of light intensity at the surface of the moss turf within each of the index categories present at a particular site. In areas lacking a tree canopy (i.e., at sites 1, 2, 3, and 9), paired meter readings were taken; the first at the surface of the herbaceous canopy, and the second at the surface of the moss turf. Percent incident light for a given subsample was determined from the mean values obtained for the relevant index category at a particular site.

Moss species composition. Species composition within a subsample was determined for the six species under study. All stems within a subsample were separated from each other and individual stems (=ramets, sensu Sarukhán and Harper 1973) were assigned to the appropriate species based upon suites of morphological characters (Watson 1974). Clonal affinities could not be deter-

mined. In areas rich in *Pa. pallidisetum* and *Pa. formosum* (species which are virtually identical in gross morphology), leaves on all stems in the subsample were dissected to ensure accurate identification. All stems considered in this study are on deposit in the Bryological Herbarium of the Missouri Botanical Garden, St. Louis, Missouri.

Computation of Indices of Niche Breath and Overlap. Values of niche breadth and microhabitat diversity were computed as $1/n\Sigma\, p_i^2$ (Levins 1968, Colwell and Futuyma 1971), and as described in Watson (in press). Indices of niche overlap were computed using the symmetrical index of Pianka (1973, and see May 1975 and Watson, in press for discussion). Due to interaction among the habitat parameters, indices of overall niche breadth and overlap were computed as summation values (Watson in press, May 1975). Indices were computed for each species at each site. Comparisons were made among species within sites and for individual species among different sites. Habitat diversity among sites was also compared.

Results

General Patterns of Vegetational Distribution on the Mountain

Polytrichaceous moss cover varied among sites from a high of 52% at summit site 1, to a low of 8% on the exposed shoulder at site 3 (Table 2). Maximum moss densities were achieved on the open sites (i.e., sites 1, 2, 3, and 9). Density decreased with decreasing altitude. Seventy percent of the moss stems examined were collected from the open sites above 1,250 m. Only 21% of the stems evaluated were collected from the forested regions of the mountain.

The compositions of the understory community also varied with altitude (Table 2). Herbs made important contributions to the understory community both at the open sites, and at a number of the forested sites (i.e., sites 5 and 6). At site 4, other bryophytes formed the dominant vegetation within the understory canopy; while at sites 6, 7, and 8 a significant amount of ground remained uncolonized, probably due to the sizeable accumulation of leaf litter at these sites. Bare ground was a significant component of the understory community at sites 3, 7 and 8. At site 3, bare ground was probably maintained due to harsh environmental conditions at the site which made establishment and spread of plants difficult. At sites 7 and 8, bare ground was more likely maintained because of substrate instability.

Individual sites could be identified as centers of distribution for particular moss species. Ninety percent of the stems of *Polytrichum commune* were collected at sites 2 (and 9), 91% of the stems of *P. juniperinum* at sites 1 (and 2), 85% of the stems of *P. piliferum* at site 3. Species of *Polytrichastrum* exhibited broader patterns of distribution within the forested regions of the mountain. Eighty-four percent of the stems of *Polytrichastrum formosum* were collected at sites 2–7, 75% of *Pa. pallidisetum* at sites 5, 7, and 8, and 69% of *Pa. alpinum* were collected at sites 5-8.

Patterns of Microhabitat Diversity Among Sites

Estimates of within site microhabitat diversity, *as experienced by the six species under study,* were obtained from the distributions of the subsample quadrats along the four microhabitat parameter axes (Table 2). Variation among sites was observed both in the

Table 2. Diversity measures along the gradient (diversity $= 1/n\Sigma p_i^2$)

| Site | Community understory diversity[a] | Polytrichaceous moss diversity[b] | Microhabitat Diversity | | Soil | | |
			% Incident light[a]	Substrate	Texture	pH	Overall[e]
1	0.37	0.18	0.24	0.23	0.13	0.34	0.24
2	0.55	0.45	0.37	0.20	0.13	0.25	0.24
3	0.70	0.29	0.25	0.25	0.22	0.30	0.26
4	0.39[c]	0.22	0.16	0.69	0.14	0.36	0.34
5	0.69	0.48	0.24	0.36	0.13	0.42	0.29
6	0.62[c]	0.26	0.15	0.32	0.13	0.34	0.24
7	0.54	0.30	0.13	0.72	0.29	0.49	0.41
8	0.43	0.39	0.13	0.59	0.42	0.42	0.39
9	0.30[c]	0.54	0.15	0.20	0.51	0.28	0.29

[a] Based on data adjusted to a cumulative frequency of 1.0 summed across all vegetational classes < 35 cm tall (including polytrichaceous moss, other bryophytes, herbs, woody plants, leaf litter, bare ground)

[b] Based on the relative abundances of the six subject species at each site

[c] Underestimate due to missing data

[d] Computed for 8 categories of % incident light as discussed in Watson (in press)

[e] Computed as the mean value due to the apparent interdependence of the four habitat parameter axes (see Watson in press 1, May 1975)
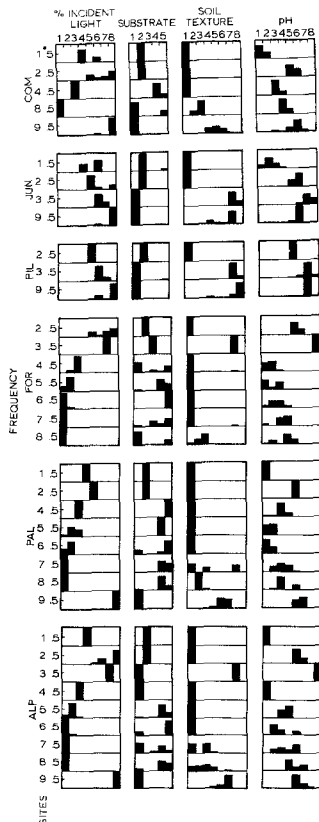

Fig. 1. Comparison of the distribution patterns of each species across the four habitat parameter axes at the different sites along the altitudinal gradient. Values sum to 1 horizontally, indicating the relative abundance of the species within the different microhabitat categories at each site. COM = *Polytrichum commune*, JUN = *P. juniperinum*, PIL = *P. piliferum*, FOR = *Polytrichastrum formosum*, PAL = *Pa. pallidisetum*, ALP = *Pa. alpinum*

amount of within site microhabitat diversity and the position of the dominant microhabitat category along each of the habitat parameter axes. Overall microhabitat diversity varied among sites from a low of 0.24 at sites 1, 2 and 6, to a high of 0.41 at site 7. There was no significant correlation between overall microhabitat diversity at a site and either understory community diversity or the diversity of the polytrichaceous moss flora at a site (Table 2).

Patterns of Species Distribution Along the Four Habitat Parameter Axes at the Different Sites Along the Altitudinal Gradient

Each of the six species displayed unique patterns of distribution along each of the habitat parameter axes which, with the exception of their patterns of distribution along the substrate axis, were observed to vary in location among sites (Fig. 1, Table 3).

There was no significant correlation between the relative abundance of a species at the different sites along the altitudinal gradient (see Watson 1979), and the overall niche breadths of the species at each site (Table 4). Furthermore, there was only a weak correlation between the relative dominance of a species at a site, and the overall niche breadth of the species at that site ($r = 0.41$, $p < 0.01$). These data suggest that niche breadth is not a function of the dominance status of a species (either with respect to the proximity of the species to its distribution center, or the dominance of that species within a particular site); that is, dominant species do not have predictably wider (or narrower) niche breadths.

Discussion

In a related paper dealing with ecotope relationships (sensu Whittaker et al. 1973) among the six polytrichaceous moss species considered above, a number of criteria, based upon species distribution patterns, were suggested for assessing the importance of com-

Table 3. Habitat occupation of the species within each site (represented by the weighted mean ± 1 S.D.)[a]

% Incident Light

Site	Polytrichum commune	Polytrichum juniperinum	Polytrichum piliferum	Polytrichastrum formosum	Polytrichastrum pallidisetum	Polytrichastrum alpinum	Mean variance (S.D.) among species within site[b]	Habitat mean ±1 S.D. within site[c]
1	63±8	68±8	—	—	*	*	8	65±9
2	79±8	73±7	*	80±7	*	83±6	7	77±8
3	—[j]	75±2	75±2	*	—	*	2	76±3
4	*[j]	—	—	12±3	14±1	*	2	13±3
5	—	—	—	6±1	8±2	7±1	1	7±2
6	—	—	—	4±1	6±1	4±0.37	1	4±1
7	—	—	—	4±0.38	3±0.44	4±1	1	4±1
8	*	—	—	5[k]	5	5±0.32	0.10	5±1
9	86±3	87±1	84±4	—	86±0.50	86±1	1	86±3
Mean variance (S.D.) among sites for a species[d]	6	6	3	2	1	2	3[f]	3.7[g]
Species distribution on the mountain[e]	79±12	70±9	76±4	15±22	14±22	28±36	18[h]	37±36[i]

Soil pH

Site	Polytrichum commune	Polytrichum juniperinum	Polytrichum piliferum	Polytrichastrum formosum	Polytrichastrum pallidisetum	Polytrichastrum alpinum	Mean variance (S.D.) among species within site[b]	Habitat mean ±1 S.D. within site[c]
1	3.57±0.10	3.67±0.10	—	—	*	*	0.10	3.68±0.15
2	4.30±0.10	4.35±0.09	*	4.28±0.10	*	4.28±0.13	0.10	4.31±0.10
3	—	4.68±0.13	4.65±0.10	*	—	*	0.12	4.67±0.12
4	*	—	—	3.59±0.10	3.76±0.10	*	0.10	3.65±0.17
5	—	—	—	3.55±0.22	3.58±0.12	3.93±0.10	0.15	3.68±0.25
6	—	—	—	3.70±0.17	3.50±0.14	3.81±0.23	0.18	3.76±0.19
7	—	—	—	3.90±0.16	3.86±0.17	3.99±0.26	0.30	3.93±0.25
8	*	—	—	4.05±0.21	3.93±0.22	4.21±0.20	0.21	4.15±0.23
9	4.39±0.17	4.45±0.08	4.42±0.04	—	4.31±0.10	4.26±0.11	0.11	4.36±0.16
Mean variance (S.D.) among sites for a species[d]	0.12	0.10	0.07	0.16	0.14	0.17	0.14[f]	0.18[g]
Species grouped mean ±1 S.D.[e]	4.27±0.25	3.89±0.37	4.61±0.13	3.80±0.37	3.79±0.28	4.07±0.30	0.28[h]	4.04±0.40[i]

[a] weighted means are calculated by including the number of stems found in each category

[b] mean site variance among species is calculated by averaging the variances exhibited by all species within a particular site

[c] habitat means ±1 S.D. are calculated from the distribution of the subsamples within each site across the habitat axis

[d] means species variance among sites is computed by averaging the variances exhibited by a single species at each of the sites in which that species occurs

[e] species distribution along the habitat parameter axis, on the mountain considered as a whole, is computed as a weighted mean ±1 S.D. as described in (a)

[f] mean variance in habitat occupation among species within sites is computed by averaging the values computed in (b)

[g] mean variance in habitat availability for all sites is computed by averaging the values of S.D. computed in (c)

[h] mean variance in patterns of habitat occupation for all species on the mountain are computed by averaging the values of S.D. obtained in row (d)

[i] mean variance in habitat availability on the mountain is computed from the distribution of all subsamples at all sites on the mountain. Value is given as mean ±1 S.D.

[j] symbols: —species not present at site; * species is present in no more than 2 subsamples at a particular site

[k] no variance is indicated if 3 or more subsamples containing a species at a particular site occur in the same position along the habitat parameter axis

petitive interactions among bryophyte species in determining their relative patterns of microhabitat occupation (Watson in press 1, 1980).

If competitive interactions among species are of importance in regulating community composition by determining the relative distributions of species along environmental or microenvironmental gradients, then the following predictions may be made concerning patterns of microhabitat occupation by the species under differing sets of environmental conditions. 1. The distance (d) separating the centers of the species' distributions along particular habitat

Table 4

Site	% Incident Light (8)	Substrate	Soil Texture	Soil pH	Mean Overall
(a) Mean Niche Breadths of Species					
1	0.18	0.21	0.20	0.20	0.20
2	0.26	0.20	0.20	0.19	0.22
3	0.17	0.21	0.16	0.18	0.18
4	0.14	0.29	0.13	0.20	0.19
5	0.23	0.33	0.13	0.26	0.24
6	0.17	0.30	0.13	0.31	0.23
7	0.13	0.50	0.25	0.36	0.31
8	0.13	0.37	0.28	0.26	0.25
9	0.15	0.20	0.27	0.20	0.21
(b) Mean Overlap of Species					
1	0.418	0.116	1.000	0.729	0.57
2	0.276	1.000	1.000	0.548	0.71
3	0.774	0.265	0.755	0.666	0.62
4	0.393	0.262	0.459	0.319	0.34
5	0.582	0.565	1.000	0.286	0.61
6	0.581	0.320	1.000	0.125	0.51
7	1.000	0.376	0.307	0.422	0.54
8	1.000	–	0.372	0.536	0.64
9	0.736	1.000	0.275	0.462	0.62
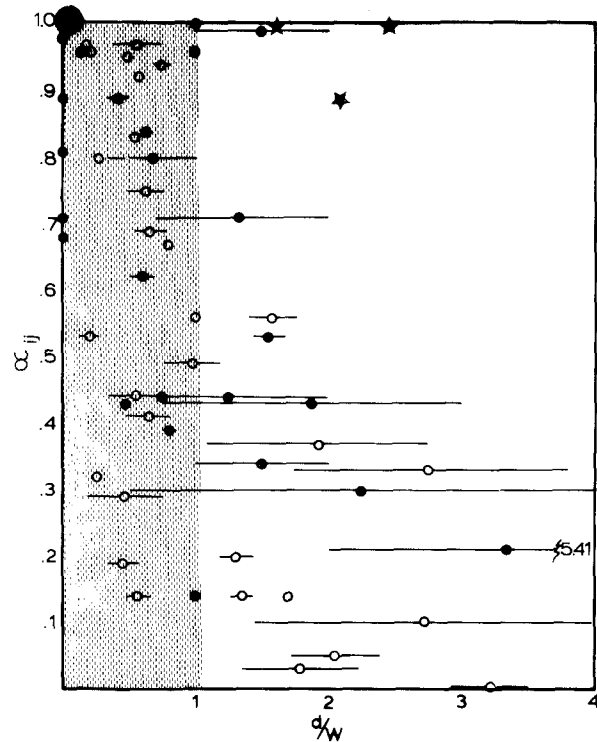
Fig. 2. Relationship between mean d/w and the symmetrical overlap function (α_{ij}) along the dimensioned habitat parameter axes of soil pH and % incident light. Mean values of d/w have been plotted because the values are asymmetric. Endpoints of the solid lines represent the actual values of d/w for each member of the species pair. The crosshatched area represents the region in which values of d/w are less than 1. ● values determined along the axis of % incident light; o values determined along the axis of soil pH. All values were computed from data for species pairs within the individual sites. Note that several values of α_{ij} depart from the predicted relationship of decreased α_{ij} with increasing values of d/w (i.e., the starred points). These points represent species pairs which were closely adjacent to each other along the habitat parameter axis of % incident light, but which exhibited extremely low variance in their utilization functions, resulting in large values of d/w despite their close packing

parameter axes at each site should be greater than, or equal to, the variability in the utilization functions of the individual species along these axes at each site (i.e., $d/w \geqq 1$, May and MacArthur (1972), May (1973)). 2. If habitat partitioning occurs among interacting species within sites, then overap (α_{ij}) among species in patterns of microhabitat occupation should decrease with increasing frequency of contact among species within sites. And, in consequence, 3. the utilization functions (or niche breadths) of the species may be expected to decrease as the diversity of species in the community increases; presumably due to exclusion of certain species from portions of their fundamental niche spaces (see Hutchinson 1957; Vandermeer 1972; Whittaker et al. 1973; and Watson 1980, in press).

It should be noted that a certain ambiguity exists in the interpretation of indices of niche overlap (see Pianka 1975, Brown and Lieberman 1973). Because of the mathematical derivation of overlap indices from the Lotka-Volterra competition equations (see Hutchinson 1978), many authors equate values of α_{ij} with measures of the intensity of competition among species pairs. Estimation of alpha in the field, however, does not provide information about the dynamic aspects of competitive interaction among two species, but rather, the degree to which two species mutually utilize a particular set of resources (or microenvironments). Pianka (1973, 1975) and Colwell and Futuyma (1971) suggest that it may be more realistic to expect that the coefficient alpha, when used as a field measure of niche overlap, will vary inversely with the intensity of competition among species. (See Watson (1980) for a more comprehensive discussion.)

In the analysis of ecotope relations among these six species, evidence for the role of competitive interaction, among adult plants, in regulating the relative distributions of these species was weak. Alternative hypotheses were entertained to explain the differential patterns of distribution among the species; including the physical tolerance ranges of the species, the role of juvenile interac-

tions (Watson 1981), and the importance of disequilibrium processes (Watson 1980). The possibility remained that evidence of competitive interaction among species was obscured by other factors which were more readily quantified when the behavior of the species was considered over the entire altitudinal gradient.

In this paper, analysis has been restricted to observations of the patterns of microhabitat occupation of the six species within single, visually homogeneous sites. It was hoped that comparisons made under these more uniform conditions would reveal evidence of interaction among species, if such interactions occurred with sufficient intensity to detect.

A graph of the relationship between values of d/w and niche overlap (α_{ij}) among species pairs along the two, dimensioned habitat parameter axes of incident light and soil pH for all species pairs, at all sites, is presented in Fig. 2. A negative relationship between niche overlap and values of d/w is observed, as would be predicted from a hypothesis of competitive control, assuming that the index α_{ij} actually provides a measure of intensity of competition. In contrast to expectations, however, values of d/w were
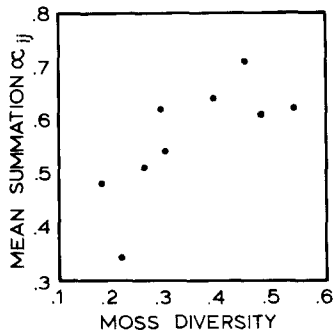
Fig. 3. The relationship between moss diversity (of the six subject species) at each site and the mean overall summation overlap among species at each site. ($y=0.82+0.52 \log x$, $r=0.77$, $p<0.01$)
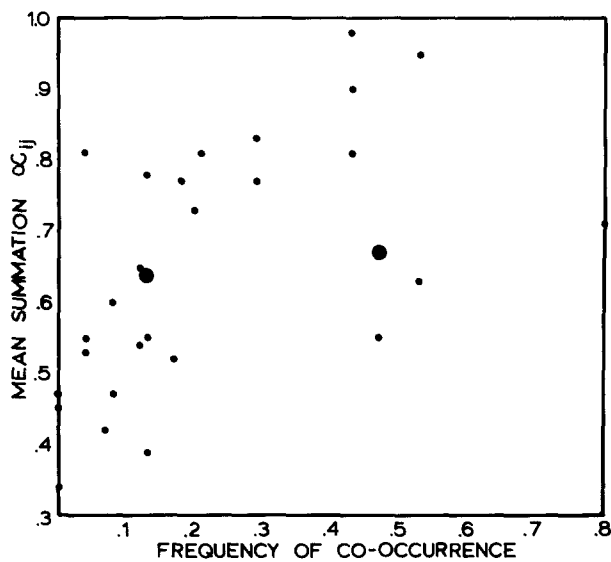

Fig. 4. The relationship between the frequency of co-occurrence of a particular species pair within a site (measured as the proportion of subsamples at a site in which both species are found) and the overall summation overlap (α_{ij}) of the species at that site. ($y=0.77+0.13 \log x$, $r=0.61$, $p<0.001$)

frequently less than 1, even for non-adjacent pairs along the dimensioned habitat parameter axes (% incident light, 17/32 or 53%; soil pH, 18/30 or 60%), indicating that species packing was much tighter than would be predicted from competition theory.

A weak positive relationship was observed between mean overall overlap and moss species diversity at a site (Fig. 3 $r=0.63$, $p<0.05$) which was of borderline significance; while their was no significant correlation observed between moss species diversity and the mean overall niche breadth of moss species at a site.

Similarly, a weak positive relationship was observed between the frequency of co-occurrence of particular species pairs within sites (measured as the proportion of subsamples at a site in which both species were found) and the overall overlap (α_{ij}) among these species pairs (Fig. 4, $r=0.54$, $p<0.01$). Circularity in the computation of frequency of co-occurrence and niche overlap was avoided

because (a) overlap was computed from the distributions of the two species in all subsamples collected at the site (i.e., including those subsamples in which the particular species was found either growing alone, or with other of the five subject species), and (b) less than half of the subsamples in any one site contained both members of the species pair growing together. Thus the data used in the computation of these indices were drawn from different distributions.

Correlations were also determined between understory community diversity (i.e., the diversity of the understory community as a whole, as computed in Table 2), and the average niche breadths and niche overlaps of the subject species at each site, in order to evaluate the importance of unrelated co-occurring species to the determination of patterns of microhabitat occupation by the six subject species. No significant correlations were found, suggesting that the diversity of the understory community did not influence the patterns of microhabitat occupation of these six species. Competition from unrelated coinhabitants for microhabitats sites, if occurring, did not exert an obvious influence upon observed moss community structure.

Thus, even when observations of the patterns of inter-relationship among these six moss species are examined within sites, strong evidence of a central role for competition among species in the determination of community structure, is lacking. No contraction in the utilization functions of the species is observed with increasing community complexity, nor is niche overlap reduced. In fact, the opposite pattern is more frequently observed, in which niche overlap increases with increasing community complexity. Even the observations of high overlap values with low values of d/w cannot be viewed as support for the hypothesis of competitive control of community structure. For, as discussed above, high overlap values may in fact be more indicative of absence of competition among species along the particular habitat axis; species co-occurring broadly with each other due to the lack of mutual interference. If competition among species is occurring, it has not resulted in habitat partitioning among them. An alternative hypothesis may be proposed to explain the observed patterns of distribution of these six moss species; based upon the following observations.

As noted earlier, readily discernible shifts in patterns of microhabitat occupation by the individual species are observed along the altitudinal gradient (Fig. 1, Table 3). Concommittant with this shift in location of the utilization functions of these species, are shifts in the range and distribution of microhabitat categories within sites as these distributions are examined along the altitudinal gradient (Fig. 1, Table 3). The variation in microsite distribution among sites results in differences among them both in their degrees of microhabitat diversity and in the locations of their dominant microhabitat categories along each of the habitat parameter axes. Strong positive correlations are observed between the patterns of distribution of the individual species (computed as the weighted mean ± 1 S.D. of the species distribution along particular dimensioned habitat parameter axes) and the distribution of the subsamples across these axes within each site (% incident light, $r=0.96$, $p<0.001$) (Table 3).

Furthermore, the niche breadths of the species along the four habitat parameter axes vary among sites (Table 4a). A positive correlation is observed between the mean overall niche breadth (computed as the average of the overall niche breadths of the individual species at each site) and the overall microhabitat diversity of a site ($r=0.70$, $p<0.05$); indicating that the average niche breadths of the species at a site increase as the amount of overall microhabitat diversity at that site increases.
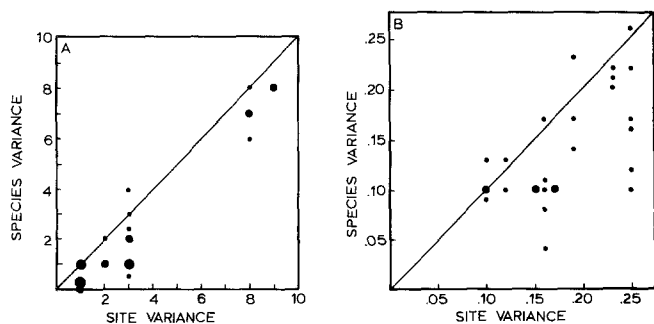
Fig. 5A and B. Relationship between variance in microhabitat availability (or utilization by the species group) at a site and the variability in habitat occupation by the individual species at each site. Data taken from Table 3 as discussed in text. Line drawn is of a 1:1 relationship between site variance and species variance. **A** % incident light, **B** soil pH. Fitted regressions were as follows: % incident light, $y=0.62+0.94\ x$, $r=0.96$, $p<0.001$; soil pH, $y=0.03+0.63\ x$, $r=0.61$, $p<0.001$)

Similarly the mean niche breadths of the species at the site (computed as the average of the individual species niche breadths) along each of the habitat parameter axes, considered individually, are positively correlated with the amount of microhabitat diversity at the site (% incident light, $r=0.90$, $p<0.001$; substrate, $r=0.83$, $p<0.01$; soil texture, $r=0.83$, $p<0.01$; soil pH, $r=0.78$, $p<0.05$); indicating that as microhabitat diversity increases along the individual habitat parameter axes, the average niche widths of the species along those axes also increases.

There is no correlation between microhabitat diversity along particular habitat parameter axes at a site and the amount of overlap among species in their patterns of microhabitat occupation at that site (Table 4b). Similarly, there is no correlation between the amount of mean microhabitat diversity at a site and the amount of mean overall overlap among species at that site; also indicating that increasing environmental complexity does not result in an increase in habitat partitioning among the co-occurring species.

Similarly, there is a strong positive correlation between site microhabitat variance and the variance in utilization functions of the individual species within sites across the dimensioned habitat parameters of % incident light and soil pH (Table 3, Fig. 5). These data, considered together, suggest that these bryophyte species occupy an increasing range of microhabitats, as these habitats are made available to them along the altitudinal gradient, and thus may be considered to behave opportunistically (sensu Slack 1977, Tramer 1967, Watson 1980).

The data suggest that an alternate hypothesis to that of competitive control of community structure may better explain the patterns of species distribution along the altitudinal gradient observed in this study. The hypothesis, in its simplest form, may be stated as follows: that patterns of species distributions are largely a function of the availability of a range of appropriate microhabitat states. That community composition is a product of interaction among several factors, including; establishment order, dispersal ability, competitive abilities of juvenile and adult plants, and persistence time of colonized habitats. Such a non-equilibrium theory of community structure has recently been proposed and discussed in detail by Huston (1979).

The applicability of this hypothesis for consideration of moss community structure is predicated on a number of assumptions which appear to be supported in the literature, among them: the ability of moss spores to disperse readily through the environment such that the chances of spores reaching a wide array of different microenvironments is high (Slack 1977), the apparent ability of bryophyte spores to establish in a wide array of different microhabitats (Apinis 1939; Watson personal observation), the ability of bryophyte species to persist in a range of physical environments (see Slack 1977; Lee and LeRoi 1979) presumably due, in part, to environmental buffering within intact moss turfs (Longton and Greene 1967), and the relatively brief persistence of moss habitats relative to the growth rates of these organisms.

Clearly competition as a controlling factor of community composition cannot be ruled out until a study of the dynamic interactions within and among species through time, is undertaken (Werner 1976). In particular, attention must be paid to interactions which may be occurring during the juvenile stages of development; for, because of the profound differences in morphology between juvenile and adult forms, unanticipated controlling factors in the environment may typically be ignored. In addition, more sophisticated statistical analyses such as those employed by Inger and Colwell (1977) may be able to more effectively separate affects of habitat availability and competition upon the values of niche breadth and overlap among species distributed along complex environmental gradients.

That such a separation is relevant is suggested in comparisons of the distribution patterns of the six species on the two, dimensioned habitat parameter axes of % incident light and soil pH which point out interesting differences in the relationships between the variances of their utilization functions within sites, and the variance in microsite availability observed within each site (Table 3). Along both habitat parameter axis, the variance in the utilization functions of the species are generally less than the microhabitat variance within the site (Fig. 5). That is, species exhibit less variance than would be expected if they were responding to the environmental mosaic in a fine-grained way, taking microhabitat sites in the frequency that they were available in the habitat. This observation suggests that patterns of distribution of the species are not simply the result of stochastic processes; but that some habitat partitioning may be occurring within this species group, greater habitat partitioning occurring along the habitat parameter axis of soil pH, where values of species variance fall well below the line indicating a 1:1 correspondence between site variance and species variance.

Whether or not the observed pattern of habitat partitioning among species with respect to soil pH is the result of competitive interactions among adult plants is not clear. The body of evidence presented above, suggests that such interactions among adults are not likely to be limiting the relative distributions of these six moss species. The contradictions implied in these observations suggest that subsequent studies should focus upon the role of soil pH in determining the structure of these bryophyte communities. Work by myself (Watson 1981) and others (Apinis 1939; Bopp 1963) suggest that attention might be profitably focused upon patterns of response among species during the juvenile stages of the life cycle.

In a related analysis (Watson in press) it was noted that the factors involved in ecotype separation among species differed in the two genera. *Polytrichastrum* species subdivided the habitat according to substrate and % incident light, while *Polytrichum* species utilized soil texture and pH. Such relationships might result from increased site microhabitat heterogeneity for these particular habitat parameters in sites dominated by one or the other genus. When comparisons of site microhabitat heterogeneity were made

among the individual habitat parameter axes, at sites dominated by either *Polytrichum* (sites 1, 2, 3, and 9) or *Polytrichastrum* species (sites 4–8), no patterns emerged; that is, sites 1, 2, 3, and 9 did not exhibit higher levels of microhabitat diversity in either soil texture or soil pH; nor did sites 4–8 exhibit higher levels of microhabitat diversity with respect to % incident light, as might have been anticipated from our previous results (Watson in press), had habitat partitioning played a significant role in structuring the community.

Conclusion

It would thus appear that moss community structure, at least in the case considered here, is not a function of competitive interaction among the component species. Patterns of microhabitat occupation appear to be strongly influenced by the availability of different habitat microsites. Individual species are exceedingly plastic in their patterns of response.

The data considered above emphasize the fact that marked changes in niche location of a species may occur when patterns of species distribution are examined along complex altitudinal gradients. Presumably species are occupying different portions of their fundamental niche spaces. The important fact which is noted here, is that the location of a species' realized niche (Hutchinson 1957, 1978; or post-interactive niche of Vandermeer 1972) is not necessarily a function of competitive interaction among species for limited habitat microsites. In many plant communities there is an overabundance of microsites, that is, not all available habitats are filled – and factors relating to access and microhabitat availability are more likely to be critical (Huston 1979; Slack 1977). This paper suggests a broader interpretation of the realized or post-interactive niche in which factors relating to microsite availability and persistence, as well as the dispersal abilities and growth characteristics of the species, may be implicated in determining the boundaries of the realized niche space.

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